NATURAL HISTORY MISCELLANEA

Published by

The Chicago Academy of Sciences

Lincoln Park-2001 N. Clark St., Chicago 14, Illinois, U.S.A.

No. 184 **December 28, 1966**

The Systematic Position of the Group of Snake Genera Allied to *Anomalepis*

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The systematic position of the small group of snakes of the "typhlopoid" genera *Anomalepis, Helminthophis, Liotyphlops* and *T yphlophis* has been a matter of controversy ever since Taylor (1939) erected a new family for *Anomalepis*. Evidence that could be held by all concerned as conclusive has not been hitherto available. Our preliminary study of the gross anatomy of members of these genera has, however, provided new information of considerable significance that strongly supports the validity of family rank for the group. Studies of the microscopic anatomy of several members of this family are in progress by the senior author, and can be expected to provide still further anatomical evidence suggesting an evolutionary hiatus between the Anomalepididae and the other typhlopoid families. The new information now in hand is, however, made available in the present account, as at least a partial substantiation of the classification adopted by the junior author in his synopsis of Mexican snakes, now in preparation.

HISTORY

In 1939 Taylor erected the family "Anomalepidae" for the single genus *Anomalepis,* then consisting of but three species (five are now known) . He characterized the family as having (1) teeth on both jaws (the other typhlopoids have them on one jaw, upper or lower, but not on both) , and (2) a unique pattern of scutellation of the head.

We here point out that, in conformity with Article 29 (and Appendix D, p. 135) of the 1961 Code of Zoological Nomenclature, the proper orthography of the family name is the *Anomalepididae,* since the genitive plural of *-lepis,* from the stem of which the name must be formed, is *-lepidis.* The revised orthographic form of the name, first noted by Amaral (1954) although for the subfamily instead of family level, retains the date and authorship of the original orthography. In systematic usage the family is therefore properly known as the Anomalepididae Taylor, 1939.

Although in present perspective Taylor's action has proved to be

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another example of his remarkably perceptive genius for discrimination, Dunn (1941) completely disagreed with his erection of the family Anomalepididae, on the grounds that his action "disregards entirely the obvious characters of scalation and dentition, disregards the obvious relationship of *Anomalepis* to *Helminthophis,* and is directly contradicted by the osteology."

Tihen (1945) suggested that Taylor's proposal of the family Anomalepididae as it stood was premature, but proposed in turn that the three genera *Anomalepis, Liotyphlops,* and *Helminthophis* constitute a taxonomic unit and that they have a large number of characteristics in common. Tihen regarded these characteristics as placing the group nearer to *Typhlops* than to *Leptotyphlops,* and accordingly proposed that the subfamily Anomalepinae (i.e., by proper spelling, Anomalepidinae) be recognized, and that it consist of the three genera above. This subfamily, with the subfamily Typhlopinae (consisting of two genera, *Typhlops* and *T yphlophis)* , by his scheme comprise the family Typhlopidae. The family Leptotyphlopidae he retained unchanged, with the single contained genus *Leptotyphlops.*

Smith and Warner (1948) , in a study of the evolution of the ophidian hyoglossum, found that the hyoglossa of Typhlops and *Leptotyphlops* are very similar in structure, whereas that of *Anomalepis* is quite distinct and unique. On this basis they concluded that the establishment of the family Anomalepididae is warranted, and proposed that this family, with the families Typhlopidae and Leptotyphlopidae, comprise the superfamily Typhlopoidea.

Amaral, however (1954) , preferred to retain Tihen's arrangement, with two subfamilies, although he placed *Helminthophis (Liotyphlops* being a junior synonym) with *Typhlops* and *Typhlophis* in the Typhlopinae, leaving only *Anomalepis* in the *Anomalepidinae.*

Romer (1956) accepted the superfamily Typhlopoidea, consisting of the families Typhlopidae (with two subfamilies, Typhlopinae and Anomalepinae) , and, doubtfully, Leptotyphlopidae, with one genus.

Dowling (1959) opposed the erection of superfamilies in the Serpentes, and also claimed that in the past various characteristics have been described as primitive in typhlopoid genera, which are, in fact, burrowing specializations.

Haas (1962) retained Tihen's arrangement despite his discovery of considerable contrary evidence. His most recent account of the anatomy of an anomalepid (1964) defers family and subfamily considerations for an account yet to be published.

NEW DATA ON POSTCRANIAL SOFT ANATOMY

Between 1948 and 1960, no really new evidence bearing upon the classification of the typhlopoid snakes came to light, despite the extensive discussions and disagreements that appeared in the literature in that in-

terval of time. The new evidence that began to accumulate in 1960, which has become intelligible with our present studies, extensively involved the soft anatomy. The senior author in 1960 described the internal anatomy of some species of T y phio ps, and drew attention to a number of unusual features, including the presence of a large ileocolic cecum, between the small and large intestine; a functional "tracheal" lung; a pair of "pseudohemipenes" and a peculiar "retrocloacal formation" in some species; an extraordinary, unpaired cloacal gland ; and the presence of but a single oviduct, the right. No equally comprehensive account, unfortunately, has yet appeared for Leptotyphlops. In 1962, Fox and Dessauer noted that it has but a single (right) oviduct, as in T yphlops. They found the oviduct basically the same in both genera, both microscopically and macroscopically apart, perhaps, from the nature of some of the uterine glands. Fox (1965) likened both genera in three unique features : the median ventral cloacal gland ; the lobed testes; and the "lizard-like extension of the sexual segment of the kidney, distal to the preterminal segment of the collecting ducts." Unfortunately data on these features are lacking for the other typhlopoid genera.

In the present work certain major features of the soft anatomy have been studied in specimens of *Liotyphlops albirostris* from the University of Illinois Museum of Natural History; of *Typhlophis squamosus, Anomalepis flavapices,* and *Helminthophis flavoterminatus* from the American Museum of Natural History; of *Liotyphlops albirostris, L. emunctus, L. petersi,* and *Helminthophis flavoterminatus* from the United States National Museum ; of *L. incertus, L. wilderi* and *L. metae* from the Museum of Comparative Zoology; of *Anomalepis dentatus* from the University of Kansas Museum of Natural History ; and of *Helminthophis frontalis* from the University of Southern California.

The results have been somewhat surprising. In all species of *Liotyphlops* examined, and in *Typhlophis squamosus,* the oviducts are paired and almost equally well developed. Both are, therefore, apparently fully functional. This unexpected condition is in sharp contrast with that found in Typhiops and Leptotyphlops, although similar to the condition in booid and colubroid genera. The right oviduct and ovary are both usually slightly longer than the left, as is normally the case in ophidians; and the right ovary has a somewhat larger number of follicles than does the left. So far as can be determined in a gross dissection there are no Wolffian ducts in the female ; however, histological examination will be necessary before a definite statement can be made on this point.

In specimens of *Anomalepis flavapices* and *A. dentatus,* and in *Helminthophis flavoterminatus,* the right oviduct is well developed whereas the left is present as a mere vestige which does not quite reach the posterior border of the left kidney. The same condition obtains in the

single female specimen of *H. frontalis* available for examination, except that not even a vestige of the left oviduct could be found. So far, no female specimens of *H. praeocularis*, the only other species of the genus known, have been available for study. It is obvious that further specimens of *Helminthophis* must be examined before we can be sure of the nature of the oviducts throughout this genus ; likewise three species of *Anomalepis* remain unknown anatomically. Unfortunately, material is scarce, and few museum specimens are suitable for histological examination. However, the distinction of the genera *Liotyphlops* and *Helminthophis* is strongly supported by the remarkable difference in structure of the oviducts in the species examined.

The alimentary canal of some specimens was not in very good condition for detailed examination, but here again an interesting trend appeared in reference to the ileocolic cecum. This cecum, which was first reported as occurring in *Typhlops* (Robb, 1960), is present in *Helminthophis* and *Liotyphlops*, but is absent from *Anomalepis;* however, in the latter species the large intestine is quite markedly more saccular than it is in *Liotyphlops* and *Helminthophis.*

In addition it is of considerable importance to record that in all the anomalepids examined the thymus gland is single and the liver multilobulate, contrary to the condition in other snakes (Underwood, 1957 : 27-28) , but the same as in other typhlopoid genera (e.g. Robb, 1960 : 196).

NEW DATA ON CRANIAL ANATOMY

Since 1960 information has also accumulated rapidly on the cranial anatomy as well as the soft postcranial anatomy, primarily through the works of Haas (1962, 1964) , whose serial sections have revealed relationships and extensive new data not detected by previous workers dealing with alizarin-stained material. Haas shows, for example (1964:8), that the puzzling "laterosphenoids" of previous workers are surely the ventral ends of the frontals. He agrees with Tihen (1945 :207) that it is the splenial which is absent in anomalepids, not the angular as maintained by List in an as yet unpublished study. The splenial is, however, rarely absent in Typhlops, always present in Leptotyphlops, occasionally fused with the "compound bone" *(fide* List) .

Much of the new information on the cranium, cranial muscles and cranial glands provided by Haas cannot be used in the present comparison because of the absence, so far, of comparable data on *Leptotyphlops* and, to a certain extent, on anomalepids other than *Liotyphlops,* as well as on non-typhlopoid snakes. Accordingly, the following discussion, of necessity, has been confined to data which, seemingly, are comparatively complete. It is to be taken for granted that many other characters remain to be evaluated, in both the cranial and postcranial anatomy.

DISCUSSION

The characters here reported, in combination with those summarized

TABLE I. Comparisons of Typhlopoid and Non-Typhlopoid Snakes

	Leptotyphlops	Typhlops	Anomalepididae			Non-typhlopoid Snakes
			Anomalepis	Helminthophis	Liotyphlops	
1. Maxilla	a. Edentulous b. Contacts premaxilla, prefrontal c. Immovable	a. Toothed b. Not so c. Movable	a. Toothed b. Not so c. Movable	a. Toothed b. Not so c. Movable	a. Toothed b. Not so c. Movable	a. Toothed b. Contacts premaxilla, prefrontal c. Movable
2. Supraorbital	absent	absent or tiny	large	large	large	present or absent
3. Splenial	present	present, rarely absent	absent	absent	absent	present
4. Lower jaw	polyodont, short and thick	anodont, long and slender	oligodont, long and slender	oligodont, long and slender	1-3 dentary teeth*	polyodont, long and slender
5. Pelvic girdle	rarely absent	rarely absent	rarely present	rarely present	rarely present**	present or absent
6. Hyoglossum	Y-shaped, deep	Y-shaped, deep	W-shaped, superficial	W-shaped, superficial	W-shaped, superficial	U- or V-shaped, superficial
7. Quadrate	relatively long	short, flat	short, flat	short, flat	short, flat	relatively long
8. Oviducts	right only	right only	right fully developed, left vestigial	right fully developed, left vestigial or absent	right and left subequal	right and left subequal
9. Ileocolic cecum	present	present	absent	present	present	absent
10. Thymus glands	one pair	one pair	one pair	one pair	one pair	two pairs
11. Liver	multilobulate	multilobulate	multilobulate	multilobulate	multilobulate	virtually non-lobulate

*Unpublished study by List
**List's unpublished study reports a reduced girdle in one specimen of *Liotyphlops*.

by Tihen (1945 :207) except as corrected above clearly warrant recognition of the anomalepids as a distinct family. In Table 1 we reproduce an adapted version of Tihen's comparison, corrected as required, and augmented by our new characters and comparisons with other snakes. In summary, we can say that anomalepids, the family rank of which we can now confirm, include all of the genera *Anomalepis, Helminthophis, Liotyphlops* and *T yphlophis.* They differ from other typhlopoids in five characters (2, 3, 5, 6, 8) , of which three (2, 5, 8) are shared with non-typhlopoid snakes (8 only partially) and two (3, 6) are unique. If anomelepids were to be placed in the same family as either *Typhlops* or *Leptotyphlops,* it would have to be with *Typhlops,* since anomalepids share with *Typhlops* (and not with *Leptotyphlops)* three characters (1, 4, 7) , whereas not a single character differing from that of *Typhlops* is shared by *Leptotyphlops* and anomalepids. However, since Leptotyphlops and *Typhlops* agree with each other, and not with anomalepids, in five characters (2, 3, 5, 6, 8) it would be more reasonable on these grounds to combine *Typhlops* and *Leptotyphlops* in one family than to place anomalepids in the same family with either. Obviously, we do not recommend such an arrangement, but it seems clear that no reasonable objection now remains to separation of the anomalepids from other snakes at a family level.

Contrary to Dowling's conclusions (1959) we here adopt the superfamily arrangement of snakes, particularly because of the magnitude of the morphological gap now evident between the typhlopoid families on the one hand and the remaining families of snakes on the other. At least characters 4, 6, 9, 10, and 11 of Table 1 differentiate these two groups, and some of these characters are of considerable phyletic weight. Unfortunately the extent of the morphological gap has not been fully explored ; Underwood (1957: 27-28) has noted a number of other possible distinctions, *e.g.* absence of a dorsal anastomosis of the internal carotid arteries, and only a right (no left) pelvic vein connecting the right renal portal and abdominal vein. Robb (1960: 206, 209, 211-2) has noted many other very important features, the systematic significance of which may be considerable but cannot be determined until the inter- and intrageneric variation is better known. The suggestion of uniqueness of typhlopoids in the absence of a spleen is refuted by Robb's (1960: 187) description of the structure in *Typhlops.* Certainly, as the anatomy of typhlopoid and other snakes becomes better known, a revelation of additional characters, aiding in definition of typhlopoid families as well as the superfamilies of snakes, is to be expected.

We accordingly view the fundamental resemblances of all "typhlopoid" snakes as overwhelmingly convincing of their common ancestry, however remote that may have been. The doubt cast upon this conclusion by McDowell and Bogert (1954: 75-89) , and maintained by Goin and Goin (1962: 285) , has been effectively dispelled by Under-

wood (1957) . On the other hand the trend towards agreement of anomalepids with non-typhlopoid snakes in some fundamental characteristics (e.g. no. 8) suggests that, indeed, this group, despite clear affinity with other typhlopoid groups, may approximate the ancestral stock of the typhlopoid-booid lines more clearly than any other living snakes. The Wallsian hypothesis of burrowing ancestry of snakes and the combination of so many primitive features in the anomalepids primitive in respect both to the typhlopoid and booid lines of evolution make very attractive the view that anomalepids are, perhaps, the most primitive of all living snakes, and closest to the lacertilian forbears of snakes, even though it is quite obvious that the existing types of anomalepids could not have given rise directly to all other snakes. The actual ancestral stock of snakes very likely combined certain features of anomalepids and booids. Each of these groups now retains independently some primitive features, over which are superimposed different specializations that became accentuated in different ways in the more advanced families in each of the two lines of evolution. A definitive evaluation of this and other hypotheses of the phylogeny of snakes remains to be made.

CONCLUSION

Contrary to other typhlopoid snakes, most anomalepids have two oviducts, subequal or unequal. This character, combined with those summarized by Tihen, establishes conclusively the validity of the family Anomalepididae, containing the genera *Anomalepis, Helminthophis, Liotyphlops* and *T yphlophis.* Like other typhlopoid snakes but unlike any other snakes, most anomalepids have an ileocolic cecum, and all have one pair of thymus glands and a multilobulate liver. These characters, combined with the common habitus and unique jaw and hyoglossal structures, establish conclusively the validity of the superfamily Typhlopoidea.

ACKNOWLEDGEMENTS

We are greatly indebted to the following persons : Mr. Marvin Keenan of Ft. Clayton, Panama Canal Zone, for the excellently preserved specimens of *Liotyphlops* he supplied, and Major Chapman Grant who kindly arranged for our contact with Mr. Keenan ; Mr. C. M. Bogert, American Museum of Natural History; Dr. Doris M. Cochran, U.S. National Museum ; Dr. E. E. Williams, Museum of Comparative Zoology; Dr. *J.* Savage, University of Southern California; and Dr. W. E. Duellman of the Kansas University Museum of Natural History, for their generosity and kindness in making material and facilities available to the senior author; and to Dr. James C. List for permission to publish a few of the observations incorporated in his monumental dissertation on typhlopoid skeletal anatomy.

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